THE GIANT CROCODILIAN SARCOSUCHUS IN THE EARLY CRETACEOUS OF BRAZIL AND NIGER

by E. BUFFETAUT and P. TAQUET

ABSTRACT. Re-examination of crocodilian remains previously referred to *Goniopholis*, from the lower Cretaceous of the Bahia basin (Brazil), shows they really belong to the genus *Sarcosuchus* (Mesosuchia, Pholidosauridae), formerly known from the Aptian of the Sahara. Resemblances between early Cretaceous African and South American vertebrate faunas anterior to the opening of the South Atlantic Ocean are stressed.

IN 1966 de Broin and Taquet announced the discovery of a new giant crocodilian, *Sarcosuchus imperator* (suborder Mesosuchia, family Pholidosauridae), in early Cretaceous continental strata of Algeria and Niger. Since then, abundant material has been collected at the Gadoufaoua locality, in the Tegama basin of Niger (Taquet 1970); it includes complete skulls and skeletons, and provides much new information on the anatomy of this African form. On the other hand, a re-examination, by E. Bufetaut, of crocodilian remains found at the turn of the century in the early Cretaceous Bahia series of the Recôncavo (or Bahia) basin, on the north-eastern coast of Brazil, shows that the successive attributions given to these fossils by various authors are erroneous. A comparison between the specimens from Brazil and those from Niger leads us to attribute the remains from Bahia to the genus *Sarcosuchus*, and to stress the similarities between the early Cretaceous African and South American continental faunas.

As early as 1860, vertebrate remains from the Recôncavo basin, among which were two different types of crocodilian teeth, were described by Allport. In 1869 Marsh erected two new species for a few isolated teeth found by Hartt in the same area: *Crocodilus hartti*, with large, finely wrinkled teeth, and *Thoracosaurus bahiensis*, with smaller, coarsely striated teeth. Later, Woodward (1888) referred other scanty remains to *Hyposaurus derbiauus*, a species described by Cope (1886) from the Late Cretaceous of Pernambuco. More important material, discovered by Mawson, was also studied by Woodward (Mawson and Woodward 1907), who then attributed all crocodilian remains from the Bahia formation to the genus *Gouiopholis*, with two species, *G. hartti* (Marsh, 1869)—which included all the newly discovered fossils— and *G. bahiensis* (Marsh, 1869). The remains of *Gouiopholis hartti*, now in the British Museum (Natural History), which have been subjected to a re-examination, comprise the anterior part of a large lower jaw (R 3423), a dorsal scute (R 3224), and two teeth (R 2983, R 3079).

Similarities between these fossils and *S. imperator* are numerous (Pl. 28). In both instances, the very long mandibular symphysis is indicative of a long-snouted animal (Pl. 28, figs. 1, 2), while in the short-snouted genus *Goniopholis* the symphysis is always short. Other remarkable resemblances between the Brazilian form and

S. *imperator* include the spatulate shape of the anterior extremity of the mandible, the relative size of the alveoli (with small first and second, and enlarged third and fourth alveoli), and the coarse ornamentation of the ventral surface of the bone. The scute found in Brazil (Pl. 28, fig. 5) is very similar to some dorsal plates of S. imperator (Pl. 28, fig. 4), which have the same general outline, likewise bear an antero-external 'peg', and possess a smooth anterior rim (which was overlapped by the preceding scute). The presence of a peg on the dorsal scutes is by no means restricted to Goniopholis, but occurs in several other crocodilian genera, such as the Jurassic teleosaurid Steneosaurus, as already mentioned by Woodward in a footnote to the 1907 article. The large teeth of the animal from Bahia are also very reminiscent of Sarcosuchus *imperator*, in their stout general shape and in the ornamentation of their enamel, consisting of fine sinuous wrinkles. Lastly, both the African and the South American forms are very large. S. imperator is one of the largest known crocodilians, with a skull up to 170 cm in length, and an estimated over-all length of 11 m. The jaw fragment from the Recôncavo basin is 43 cm long, although it is only the anterior part of the symphysis.

Thus, Woodward's attribution of the Brazilian fossils to *Goniopholis*, which was based mainly on the presence of a peg on the dorsal scute, cannot be considered as valid. In our opinion, this South American crocodilian belongs to the genus *Sarcosuchus*. In the absence of more complete material from South America, it seems acceptable to retain different specific names for the African and the South American forms, and to call the latter *S. hartti* (Marsh, 1869). However, the differences between the two forms (in the spacing of the alveoli, for instance) seem rather unimportant, so that the possibility that they may belong to the same species cannot be excluded.

There may well be crocodilians other than *S. hartii* in the Bahia series, but they are represented by very scanty remains, which do not allow a precise identification. Although Roxo (1936) tried to revalidate *T. bahiensis* on the basis of a tooth and a procoelous vertebra of uncertain origin, the occurrence of the essentially marine late Cretaceous genus *Thoracosaurus* in the early Cretaceous freshwater Bahia series is most unlikely, as already pointed out by Antunes (1964). There is also no serious reason to assume that *H. derbianus* occurs in the Early Cretaceous of the Recôncavo basin. Both identifications were made in the erroneous belief that the Bahia series was of late Cretaceous age.

Besides crocodilian remains, the fossil material from the Recôncavo basin includes the centrum of a dorsal vertebra of a carnosaur (Allport 1860), too incomplete to be compared with the vertebrae of the several carnosaurs known from Niger. Woodward (Mawson and Woodward 1907) also mentions vertebral centra which 'seem

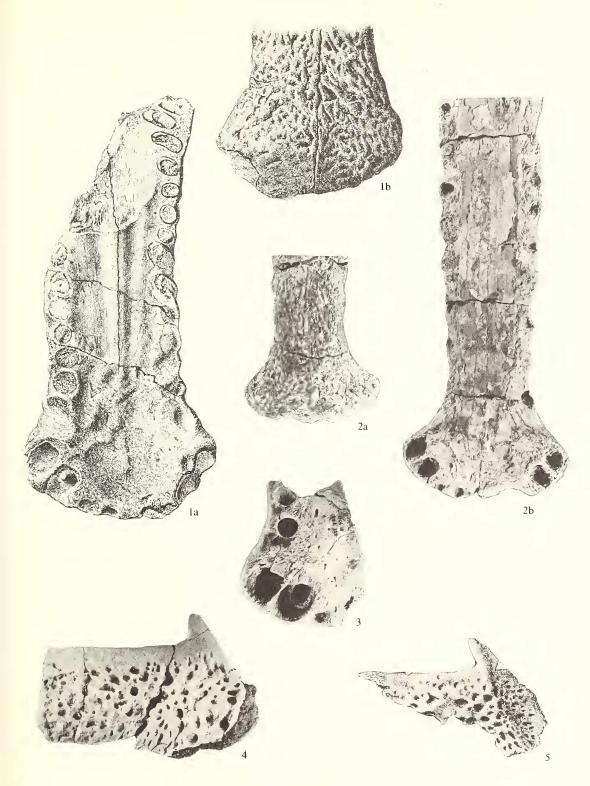
EXPLANATION OF PLATE 28

Sarcosuchus remains from Brazil and Niger, $\times 0.25$.

Fig. 5. Sarcosuchus hartti, from Brazil: dorsal scute (from Mawson and Woodward 1907).

Fig. 1. Sarcosuchus hartti, from Brazil, B.M.(N.H.) Specimen No. R 3423; anterior extremity of lower jaw (from Mawson and Woodward 1907); *a*, in dorsal view; *b*, in ventral view.

Figs. 2-4. *Sarcosuchus imperator*, from Niger. 2, anterior extremity of lower jaw of young individual; *a*, in ventral view; *b*, in dorsal view. The very spatulate shape is due to the youth of the animal. 3, anterior extremity of right dentary of adult specimen, in dorsal view. 4, dorsal scute.



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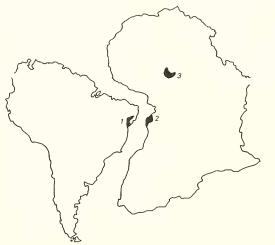
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to agree closely with the corresponding bones of Iguanodonts'; this information, if true, is interesting, since several iguanodontids are known from the Early Cretaceous of Niger (Taquet 1970). The vertebrate fauna from Bahia also includes scales of the holostean fish *Lepidotus* (with three species) and remains of two species of the coelacanth *Mawsonia* (Patterson 1975). The genus *Lepidotus* is also represented in the Tegama basin of Niger by numerous skull remains and large scales (now being studied), while a skull and several post-cranial fragments of a *Mawsonia* from the same area will soon be described by Wenz. Patterson (1975) has stressed the resemblances between the early Cretaceous fish faunas from the Recôncavo and Gabon basins. We can now parallelize the freshwater faunas from these regions with the one from the Tegama basin (Table 1), and include *Sarcosuchus* in the list of early Cretaceous genera common to South America and to Africa.

com	mon to South America	and Africa.
Recôncavo basin (Bahia series)	Gabon basin (Cocobeach series)	Tegama basin (Aptian)
Mawsonia major M. minor	Coelacanth	Mawsonia (new species)
Lepidotus mawsoni L. souzai L. roxoi	Lepidotus sp.	<i>Lepidotus</i> sp.
Sarcosuchus hartti		Sarcosuchus imperator

TABLE 1. Comparative list of early Cretaceous vertebrate genera

The Recôncavo basin is a 'semi-graben' (Fonseca 1966) which was filled, during the early Cretaceous, by the several thousand metres of freshwater sediments of the Bahia series, consisting mainly in conglomerates, shales, and sandstones. Both the lithology and the fauna of this so-called 'Gondwana Wealden' (Krömmelbein 1966) are indicative of a 'shallow lacustrine environment' (Fonseca 1966). As pointed out by Beurlen (1961), these sediments can hardly have accumulated in geographical conditions similar to the present ones, i.e. a basin open on the Atlantic Ocean. The eastern part of the graben is to be found on the West coast of Africa (text-fig. 1),



TEXT-FIG. 1. Map showing the three basins mentioned in the text: 1, Recôncavo (or Bahia) basin, Brazil. 2, Gabon basin, Gabon. 3, Tegama basin, Niger. (After Martin (1968), modified.)

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where the Gabon basin exhibits a succession of freshwater deposits (the Cocobeach series) very similar to the Bahia series (de Klasz 1965). The study of ostracod faunas from both areas shows that, according to Krömmelbein (1966), 'it seems that these ostracods lived in one single basin with completely free interchange'; this has allowed a detailed stratigraphical correspondence to be established (Krömmelbein 1971). The end of lacustrine sedimentation in the Recôncavo-Gabon graben is indicated by salt deposits of Aptian age (Reyment 1973). According to Mawson's (Mawson and Woodward 1907) and Fonseca's (1966) maps, the remains of *S. hartti* were collected in the Ilhas Formation, which belongs to the upper part of the Bahia series; they are thus probably a little older than the Aptian. *S. imperator*, from the Tegama basin, is of Aptian age. Therefore, the chronological gap between the two species is probably not very great.

The formation of the Reconcavo-Gabon graben, and of others of the same kind (Potiguar, Sergipe-Alagoas) at the beginning of the Cretaceous, is considered as an early stage in the separation between Africa and South America (Reyment and Tait 1972). The presence of the non-marine crocodilian *Sarcosuchus* in both Brazil and Niger affords additional evidence of the faunal continuity between these continents during the early Cretaceous, before the complete opening of the South Atlantic Ocean.

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E. BUFFETAUT

Laboratoire de Paléontologie des Vertébrés et de Paléontologie humaine Université Paris VI 4 place Jussieu 75230 Paris Cedex 05 France

P. TAQUET

Institut de Paléontologie 8 rue de Buffon 75005 Paris France

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